STUDIES OF NEOTROPICAL CADDISFLIES XXV: THE IMMATURE STAGES OF BLEPHAROPUS DIAPHANUS AND LEPTONEMA COLUMBIANUM (TRICHOPTERA: HYDROPSYCHIDAE)

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Abstract.—Larvae, pupae, and larval catchnets are described and illustrated for Blepharopus diaphanus Kol. and Leptonema columbianum Ulm. All data indicate that Blepharopus is closely related to, but distinguishable from, Macronema. L. columbianum is easily distinguished from its known congeners. Notes on habitats and behavior are presented.

The trichopterous family Hydropsychidae is represented in South America by two subfamilies, the Hydropsychinae and the Macronematinae. Only a single hydropsychine genus, Smicridea composed of two subgenera, is known from that continent. Larvae and pupae of several species in both subgenera have been described (Ulmer, 1909; Ross, 1944; Flint, 1974; Wiggins, 1977; etc.). Within the South American Macronematinae, however, there is considerably more generic diversity as shown by the eight known genera (Blepharopus, Centromacronema, Leptonema, Macronema, Neoleptonema, Plectromacronema, Pseudomacronema, and Synoestropsis). Our knowledge of the immature stages of these genera is very poor, however, and often based on association by elimination. Larvae of three species of Leptonema, and one species of Macronema are apparently all that have been described with firm associations of the life stages. All other generic or specific attributions are based on similarities, supposition, and elimination. We have made concerted efforts to associate by the metamorphotype method the immature stages and adults of more genera and species, but have been singularly unsuccessful with the following two exceptions.

The larvae and pupae of *Blepharopus diaphanus* Kol. are firmly associated by the presence of numerous δ and $\mathfrak P$ metamorphotypes in one collection. Their discovery removes any possibility that the larvae described by Marlier (1964) as Genus A and tentatively attributed to *Blepharopus* are that genus. Genus A in all probability is a distinctive species group of the genus *Leptonema*.

Leptonema columbianum Ulm. is associated with its larva and pupa for the first time on the basis of several female metamorphotypes. This species belongs to a group of species quite distinct from those other species whose larvae are known. Consequently it is not surprising to find the immature stages of this species showing distinct differences from its known congeners.

Blepharopus diaphanus Kolenati Figs. 1-2, 5-6, 9-24

Blepharopus diaphanus Kolenati, 1859, p. 242.—Fischer, 1963, p. 164.—Flint, 1978, p. 395, 404.

Blepharopus is a monotypic genus known from Argentina, Brazil, and Venezuela. Adults are often collected at lights adjacent to the larger rivers throughout the region. Immature stages of the genus have not been described before, in spite of the Marlier (1964) suggestion to the contrary.

The larval, pupal, and adult morphology all agree in indicating a close relationship to *Macronema*. In all the *Macronema* larvae described, each genal half possesses a carina, the two converging at the apex of the frontoclypeus. In *Blepharopus* this carina is poorly developed, and is farther from the frontoclypeal sutures at the posterior of the head than at the anterior. The head, thoracic nota, and abdomen are apparently naked, except for a few scattered long setae, whereas in most other *Macronema* species the abdomen, at least, bears a sparse covering of short, dark setae. The basic structure of the mouth parts, legs, gills, etc. seems to be the same in both genera.

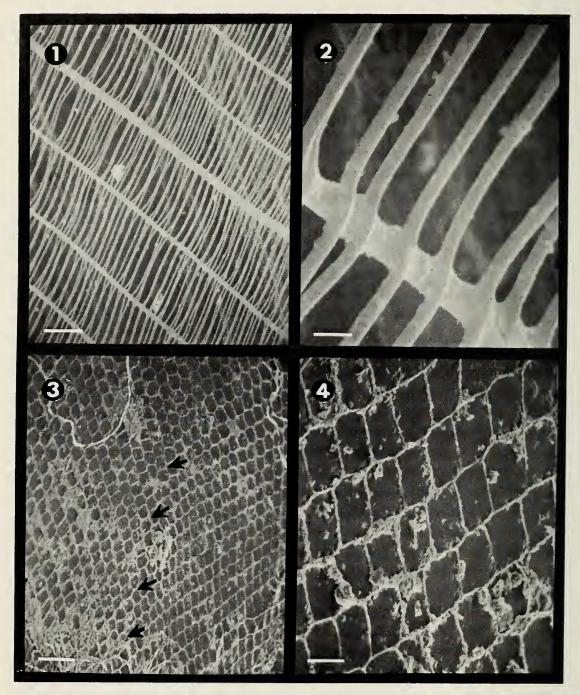
In the pupal stage there appears to be one distinctive structure, that of the raised knobs of the face which bear many long setae. There is no mention of such a structure in any of the described species of *Macronema*. The mandibles, hook plates, and apical processes seem nearly identical or only specifically different from *Macronema*.

The adult is also very closely related to *Macronema*, differing primarily in the structure of the head of the male. The protruding dorsomesal keel with bulging lateral warts is undoubtedly due to the enlargement of the eyes which have "pushed" these normally unobtrusive structures into such an obvious position. The head and thorax of the insect are extremely hairy, very different from any *Macronema* known to us.

The nets are remarkably similar to those found in *Macronema*, and are obviously adapted for sieving minute particles from the passing water. The dense brushes of the labrum and forelegs are also similar to those found in *Macronema* and are undoubtedly used in feeding on small particles captured by the net.

In sum, all life stages show a genus very closely related to *Macronema*, but with enough specializations to still deserve generic recognition.

Larva.—Length 16–18 mm, width 2.5–3 mm. Sclerites pale reddish-brown to golden-yellow, muscle scars yellow.



Figs. 1-4. 1, A portion of the catchnet of *Blepharopus diaphanus* (SEM at $500\times$; scale line at lower left = $20~\mu$ m). 2, Same, at $10,000\times$; scale line = $1~\mu$ m; note that all smaller strands overlie the larger support strand. 3, Catchnet of *Leptonema columbianum* (SEM at $50\times$; scale line = $200~\mu$ m); arrows denote approximate location of the central seam of the net. 4, Same, at $200\times$; scale line = $50~\mu$ m.

Head: Slightly wider than long; surface smooth and shining. Color pale reddish-brown, muscle scars pale yellow. Gena with a low, sharp carina from anteriad of eye almost to posterior margin; carina diverging from the frontoclypeal suture posteriad. Anterior margin of frontoclypeus slightly concave. Gena ventrally with anterior 10 stridulatory lines widely separated, the transition to the close posterior lines very abrupt. Labrum with a large membranous basal region bearing 2 transverse sclerites adjacent to frontoclypeus; with large lateral brushes on lobes; anterior margin with a dense fringe of hair; dorsal surface with scattered pale setae and a pair of long dark setae anteromesally. Mandibles strongly asymmetrical; without mesal tuft of hairs. Submentum with anterior margin concave; anterolateral angle bearing 2 large, black, setae, and a group of shorter setae.

Thorax: Sclerites pale reddish-brown, grading to golden-yellow; muscle scars pale yellow. Pronotum with 1 pair of well-developed dorsal setae, and a few anterolateral setae; smooth and shining. Prosternum broadly transverse; with a small triangular sclerite posteromesally. Meso- and metanota each with 2 pairs of erect dorsal setae, and a few laterally; surface smooth and shining. Foretrochantin broadly triangular with a marginal row of spiniform setae. Coxa of foreleg with a pad of short, spiniform setae posteromesally. Foreleg with femur bearing a slender, digitate basomesal process; femur and trochantin with a sparse fringe of long hair ventrally; tibia and tarsus with a dense fringe of long, silky, hairs primarily on outer surface. Mid- and hindlegs similar; with scattered long setae; apex of tibia with a comb of 4–5 broad, spiniform setae anteriorly. Tarsal claw of foreleg almost straight, with a spiniform basal seta; claws of mid- and hindlegs, curved, basal seta stout, arising from a produced, slightly fimbriate, pointed, basal lobe. Mesosternum with 1 pair of gills; metasternum with 2 pairs.

Abdomen: Gills ventrally, laterally, and dorsolaterally as in figure 24. Lateral line totally lacking. Integument with scattered setae; smooth and shining. Sternum 8 with 1 pair of long, dark, setae, and 1 pair of shorter, paler, setae. Segment 9 with tergum divided into a pair of small, pale, lateral plates each bearing 2 long, dark setae, and 2 short, branched setae; a small, linear, lateral sclerite with a row of long setae; sternum with a pair of ovoid plates covered with pale spiniform setae and 3 or 4 long, black setae posteriorly. At least 4 anal gills. Anal proleg short; lateral sclerite with row of long, black setae laterally; anal claw as long as lateral sclerite, curved ventrad, without accessory teeth; with 2 pale setae ventrobasally.

Pupa.—Length, ♂ 14 mm, ♀ 10 mm.

Head: Mandibles tapering regularly to a pointed apex; inner margin with 3 teeth; inflated basally, with a group of setae on outer face. Labrum small and rounded, with 2-3 basolateral setae. Face with a bilobed, protruding area whose integument is spiculate and bears a number of very long, hooked

setae on each side. Vertex with a small group of setae on each side and a pair anteromesally.

Thorax: Meso- and metanota with 1 or 2 pairs of erect submesal setae. Tibia and tarsus of midleg broad and flattened, with well-developed lateral fringes.

Abdomen: Lacking lateral fringe or lobes; gills present. Hook plates anteriorly on segments 3–8; posteriorly on segment 3. Dorsum of segment 2 and 3 regularly, but sparsely, covered with short spiniform setae; segment 4 with an irregular row of long setae along posterior margin. Apical processes tapering to a blunt point; ventral and lateral surface bearing long, pale, slightly hooked setae from well developed tubercles.

Larval catchnet.—Individual meshes 0.5 to 2.5 μ m wide ($\bar{x} = 1.85 \mu$ m; s.e. mean = ± 0.2284) and 9 to 55 μ m long ($\bar{x} = 26.3$; s.e. mean = ± 1.64). Total catchnet area ca. 30 mm²; thus, about 600,000 meshes per net.

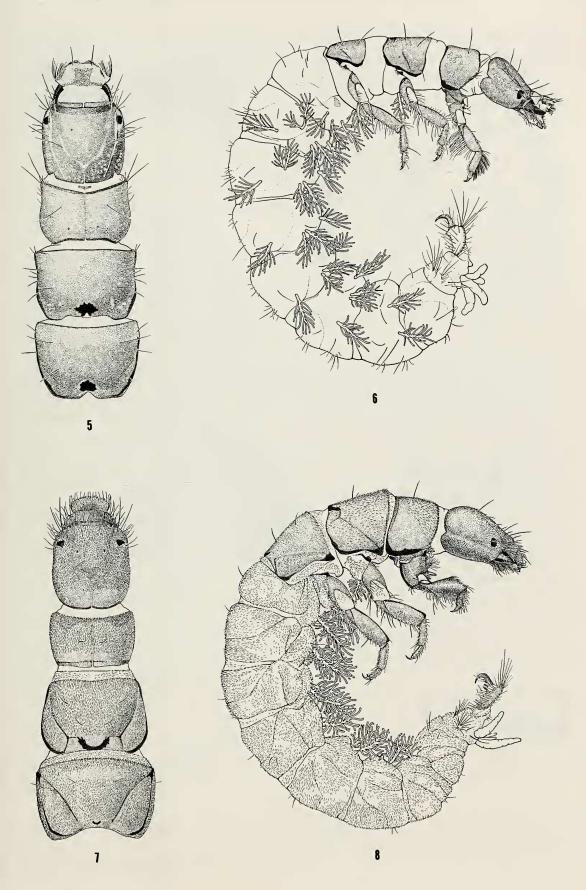
Pupal shelter.—Length approx. 15 mm, width 5 mm. Firmly constructed of small sand grains. Anterior end often "crowned" by a marginal "fence" of sand grains with a distinct closing lid. Inside of anterior lid a regular mesh-like sieve membrane attached around edge of lid; posteriorly without such a distinct lid, but internally with the same sieve membrane.

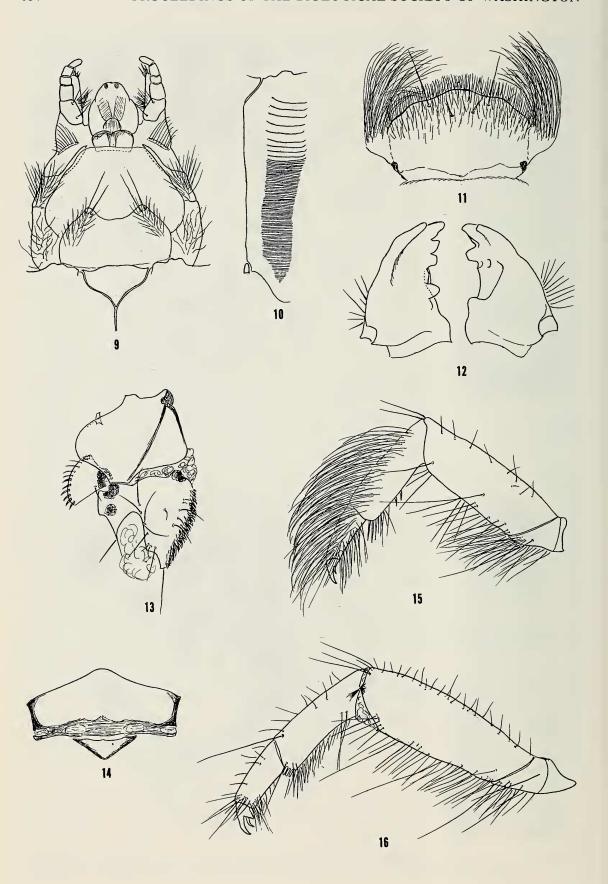
Material.—Brazil, Edo. Rio de Janeiro, Mun. Rio Claro, Rio Pirai, 8 Apr. 1977, C. M. & O. S. Flint, Jr., many hundred larvae, pupae, δ φ metamorphotypes, and adults.

Remarks.—Although the vast majority of adult collections of this species made by the senior author are from near large rivers, the situation at the Rio Pirai is quite different. This collection was made in a riffle area where the stream is only about 5 meters wide and one-third of a meter deep. The water is slightly turbid and greenish, temperature 25°C, and the bottom of the riffle composed of sand, gravel, and rubble. Below (and probably upstream also) the stream is wider and deeper, almost lotic in aspect. In common with the larger riversites, however, the stream is open everywhere to full sun with the probable consequence of higher water temperature and perhaps greater primary productivity.

Although the exact details of the larval dwelling were not noted, they were constructed of sand grains attached to stones and appeared similar to that described previously for *Macronema zebratum* Hagen (Wallace, 1975; Wiggins, 1977). The catchnets are obviously not spun in the same manner as typical Hydropsychinae (see Sattler, 1955, 1958), since the smallest

Figs. 5–8. Blepharopus diaphanus: 5, larval head and thoracic nota, dorsal; 6, larva, lateral. Leptonema columbianum: 7, larval head and thoracic nota, dorsal; 8, larva, lateral.





strands overlie the larger support strands (Figure 2). They are, however, virtually identical to those of *Macronema* (Sattler, 1963; Wallace, 1975), but the individual meshes are the smallest yet reported for the Hydropsychidae. The pupal shelters were often attached on one side to a larger stone, or rarely free in the sandy substrate.

Leptonema columbianum Ulmer Figures 3-4, 7-8, 25-38

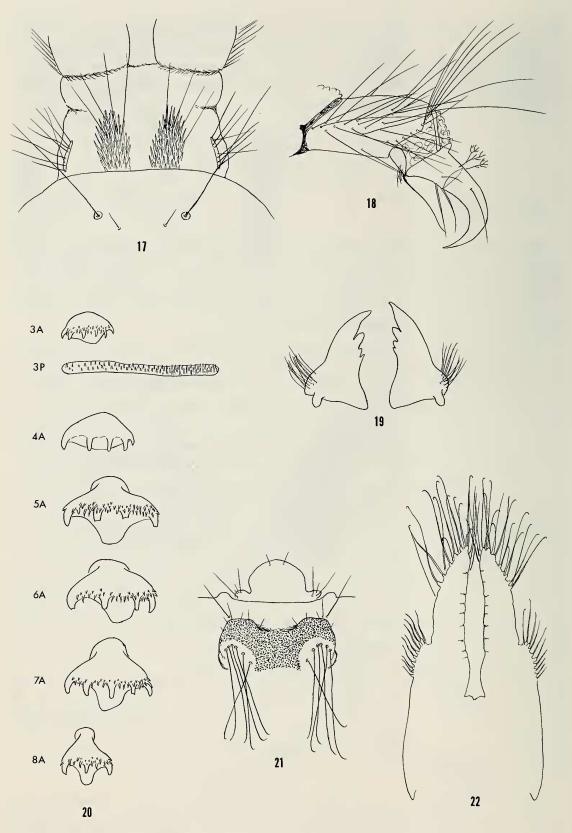
Leptonema columbianum Ulmer, 1905, p. 61.—Fisher, 1963, p. 168.—Flint, 1978, p. 385.

This is one of the more widely distributed species of *Leptonema*, occurring from Colombia to Argentina, generally on the eastern side of the Andes. Judging from adult collections, it is most frequently, perhaps exclusively, inhabiting large rivers. It has been recorded (Flint, 1978), from numerous localities in the Rio Solimões–Amazonas area.

Larvae, generally of unknown species of the genus, were first described in the late 1800's. Until now the larvae of only the following species are securely associated and described: L. albovirens (Walk.) (Flint, 1968), L. archboldi Flint (Flint, 1968), and L. eugnathum (Müller) (Müller, 1921). On the basis of these descriptions, the published descriptions of unassociated larvae, and several undescribed but associated species in the collections of the National Museum of Natural History, the larvae of columbianum possess a number of distinctive characteristics. These are primarily in the area of the foreleg, especially the coxa. The forked ventral and digitate anterior processes, between which is found a hairy lobe, produce a unique conformation of the coxa. Only Leptonema species 2 (Roback, 1966) is similar, but this is a much larger species which lacks the hairs from the lobe between the processes. Together with L. sp. 2, columbianum shares the very broad, almost circular, outline of the fore femur. In all other known species of the genus the femur, although slightly enlarged, is proportionately much more elongate. Considering the overall similarity of L. sp. 2 to columbianum, it seems quite possible that sp. 2 might be L. crassum Ulmer.

Larva.—Length 10–12 mm; width 2–2.5 mm. Sclerites golden-yellow with fuscous marking.

Figs. 9–16. *Blepharopus diaphanus*: **9**, larval maxillolabium, ventral; **10**, larval gena showing stridulatory lines, ventral; **11**, larval labrum, dorsal; **12**, larval mandibles, ventral; **13**, larval propleuron and coxa, lateral; **14**, larval prosternum, ventral; **15**, larval foreleg, anterior; **16**, larval hindleg, anterior.



Figs. 17–22. Blepharopus diaphanus: 17, larval eighth and ninth sterna, ventral; 18, larval anal proleg, lateral; 19, pupal mandibles, ventral; 20, pupal hookplates, dorsal showing abdom-

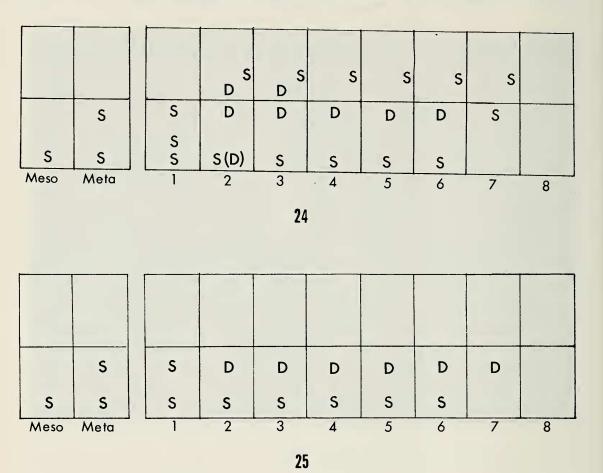


Fig. 23. Blepharopus diaphanus, biotope; Rio Pirai.

Head: Slightly longer than wide; golden-yellow, immaculate. Anterior ¾ of dorsal surface regularly covered with short, pale, blade-like setae. Anterior fourth of dorsum with scattered, long, light and dark setae. Anterior margin of frontoclypeus produced, truncate in center. Labrum transverse, surface with many, mostly pale, hairs; anterolateral angle with a short brush of hairs. Mandibles asymmetrical; left with a mesal tuft of fine hairs, with a double basal, 4 mesal, and 2 additional apicodorsal teeth; right with a double basal, 3 mesal, and 1 additional apicodorsal tooth. Submentum with anterior margin nearly straight. Anterior ventral apotome transversely triangular.

Thorax: Sclerites golden-yellow, with fuscous markings. Pronotum with 1 pair of well-developed dorsomesal setae; surface with many small, fine dark setae and very short, pale, blade-like setae. Prosternum, transversely rectangular; with a lightly sclerotized, rectangular, posteromesal lobe. Meso-

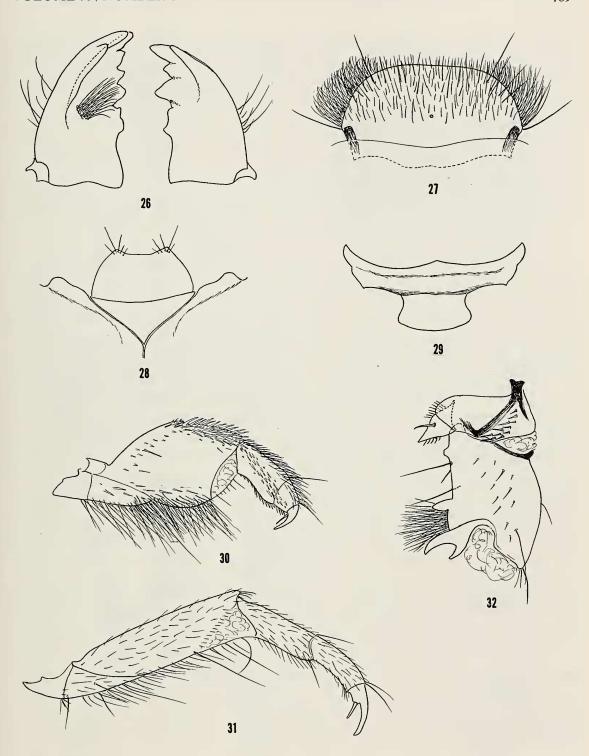
inal segment number and anterior or posterior position; 21, pupal labrum and ventral half of face, anterior; 22, pupal apical appendages, dorsal.



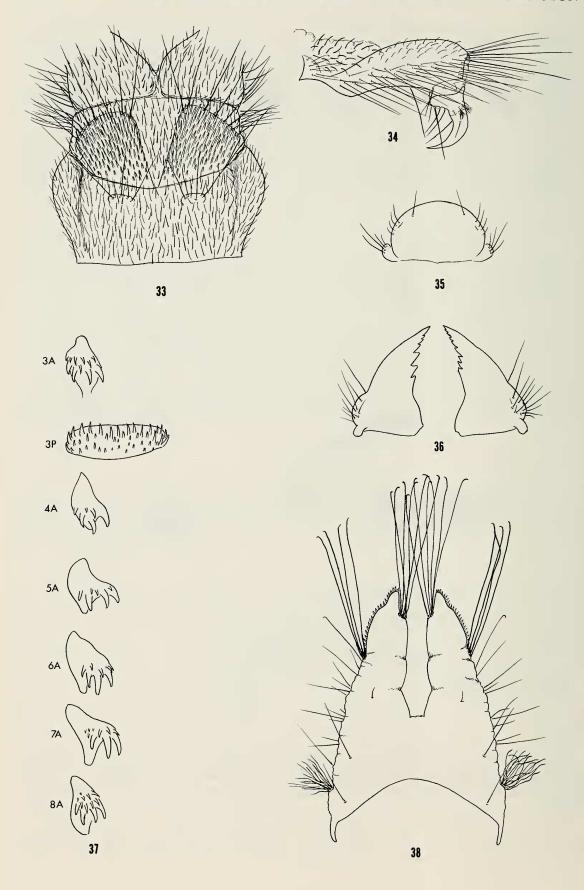
Figs. 24-25. Blepharopus diaphanus, 24; Leptonema columbianum, 25. Schematic gill diagrams of the lateral aspect of the meso- and metathorax and first 8 abdominal segments. S = a single long central filament with numerous lateral filaments; D = 2 S-type filaments with adjacent bases.

and metanota each with 2 pairs of erect dorsal setae; surface densely covered by short, dark setae. Fore trochantin tapering to an apical point, with numerous setae. Coxa of foreleg bearing a forked anteroapical process, and a digitate process on anterior margin, between processes a densely hairy lobe. Foreleg with anterior surface with pale, blade-like setae, posterior face with only a few normal setae; femur very broad, almost circular in outline. Mid- and hind legs virtually identical in shape and structure; posterior surfaces with many, pale, blade-like setae. Tarsal claw of foreleg with basal setae slender, spiniform; basal setae of mid- and hind claws very broad and enlarged. Mesosternum with 1 pair of gills; metasternum with 2 pairs.

Abdomen: Ventral gills only; as in figure 25. Lateral line virtually lacking; small tufts of hair present posteriorly on segment 3–7. Integument densely covered with blunt, slightly broadened, elongate, black setae. Segments 1–8 each dorsally with 3 pairs of long, erect setae: 1 pair sublaterally, 2nd



Figs. 26–32. Leptonema columbianum: 26, larval mandibles, ventral; 27, larval labrum, dorsal; 28, larval submentum and anterior gular sclerite, ventral; 29, larval prosterum, ventral; 30, larval foreleg, posterior; 31, larval hindleg, posterior; 32, larval propleuron and coxa, lateral.



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anteromesally, 3rd posteromesally (this group sometimes with 1 or 2 extra setae); ventrally segments 1–7 each with 1 pair of such setae sublaterally near base of lateral-most gill. Sternum 8 with posterior plates recognizable only by long, black setae they bear. Sternum 9 with a large pair of plates covered with short, golden, spike-like setae, and a row of long, black setae along posterior. Segment 9 with tergite divided into 2 small, inconspicuous, sublateral plates bearing 2 long, black setae, and a feathered seta between; with a small, round, lateral sclerite bearing many long, black setae. At least 4 anal gills. Anal proleg bearing a fringe of long, slender hairs on each side of lateral sclerite; anal claw sharply angled ventrad, without accessory teeth.

Pupa.—Length of female pupa, 9 mm.

Head: Mandibles tapering regularly to a pointed apex; inner margin regularly serrate; outer face basally with a cluster of dark setae. Labrum with anterior margin semicircular, with basolateral lobes; each lobe with a group of 4–5 setae, and anterolateral margin with a row of 5–6 setae. Front of face with a group of shorter setae anterolaterally, 2 groups of long, dark, hooked setae mesally, and a few scattered setae laterally above base of mouth parts, and behind and in front of eye. Vertex with a few dark setae on each side and anteriorly. Basal segment of antenna with a group of short setae.

Thorax: Mesonotum with a small group of setae anterolaterally; mesoand metanota each with a pair of submesal setae posteriorly. Mesothoracic legs with a hair fringe on both sides of tarsus; tibia and tarsus flattened.

Abdomen: Segments 1–7 with deeply bifid lateral membranous lobes; segment 3 with a short, single lobe. Gills ventrally. Hook plates anteriorly on segments 3–8, plates 5–7, with teeth on a distinctly elevated lobe; posteriorly on segment 3. Dorsum of segment 4 with surface sparsely covered by long, dark setae; segments 1–3 with a few short dorsolateral setae; segments 5–7 with a few, long, dorsolateral setae. Apical processes with a group of basolateral dark setae, and a scattering of lateral setae; each process with 2 groups of long, golden, hooked setae, the lateral group of 4 setae, the mesal group of 5–7; between these groups of hooked setae a short, upturned lobe covered ventrally with short, spinous setae.

Larval catchnet.—Individual meshes (Figures 3 and 4) are ca. 40.5×80 μm at the base of the net and ca. 47.5×83.5 μm at the outer net periphery.

Pupal shelter.—Length 11 mm, width 4 mm. Ovoid, ventral area attached to substrate, closed by silk. Surface evenly formed of sand grains and small

Figs. 33–38. Leptonema columbianum: 33, larval eighth and ninth sterna, ventral; 34, larval anal proleg, lateral; 35, pupal labrum, dorsal; 36, pupal mandibles, ventral; 37, pupal hookplates, dorsal showing abdominal segment number and anterior or posterior position; 38, pupal apical appendages, dorsal.

pieces of organic matter. Each end with small respiratory openings left in silk between particles.

Material.—Brazil, Edo. Amazonas, Rio Solimões, ca. 4 km upstream from junction with Rio Negro, 10 Feb. 1977, 9 larvae; Rio Solimões, nr. Ilha Jurupari, 14 Feb. 1977, 14 larvae, 1 ♀ metamorphotype; Rio Solimões, nr. Lago de Coari, 15 Feb. 1977, 7 larvae; Rio Solimões, nr. Tefé, 17 Feb. 1977, 6 larvae, 1 ♀ metamorphotype; Rio Icá, nr. junction with Rio Solimões, 23 Feb. 1977, 5 larvae; Rio Solimões, nr. São Paulo de Olivença, 27 Feb. 1977, 6 larvae, 1 ♀ metamorphotype. Peru, Dept. Loreto, Rio Amazonas, nr. junction with Rio Atacuari, 4 Mar. 1977, 3 larvae. All collected by J. B. Wallace, et al.

Remarks.—L. columbianum was the only hydropsychid larva commonly encountered in the Rio Solimões or its larger tributaries from the junction with the Rio Negro upstream to Peru. No larvae of L. columbianum were encountered in smaller streams along the main river. Larvae inhabit woody substrates consisting of fallen, submerged trees and branches along the banks of the larger rivers. Their retreats and nets are found in depressions and crevices in the woody substrate and their structure is similar to that described previously for Hydropsyche (Sattler, 1955; Kaiser, 1965). The nets of L. columbianum are of typical hydropsychid construction and possess the central seam (Figure 3) which results from the figure-eight spinning motion used in their construction (Sattler, 1955, 1958). The meshes of L. columbianum are much smaller (ca. $40.5 \times 80 \mu m$) than those made by the larva of another Leptonema species from a mountainous Costa Rican stream. This latter larva had catchnet meshes of ca. $430 \times 167 \mu m$.

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